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Social learning, culture and the ‘socio-cultural brain’ of human and non-human primates

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**Social learning, culture and the ‘socio-cultural brain’ of
human and non-human primates**

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1. Introduction

Recent decades have seen enormous strides in our knowledge and understanding of many aspects of primate social cognition (de Waal and Ferrari, 2012; Mitani et al., 2012; Seyfarth and Cheney, 2015a,b) and discoveries about primate social learning, traditions and culture have been prominent in the progress made (Whiten et al., 2011; Whiten, 2012; Hoppitt and Laland, 2013; Watson et al., in press). These latter topics provide the focus for the present review. In discussing ‘social learning’ we take a broad perspective, taking this to include all learning from others, whether from their actions or the results of those actions (Heyes, 1994). Some outcomes of such social learning may be relevant only for a short while, such as which trees are currently in fruit, but others are longer lasting and may give rise to traditions (Whiten and van Schaik, 2007). We follow Frigaszy and Perry (2003, p. xiii) in defining traditions as “a distinctive behavior pattern shared by two or more individuals in a social unit, which persists over time and that new practitioners acquire in part through socially aided learning”. Of course “two or more individuals” is a minimal criterion and traditions can be regarded as more robust the more widely they spread between individuals, between groups and through larger populations. In relation to “persists over time”, they are similarly more robust the longer they last, which may or may not involve multiple generations. ‘Culture’ is a more contentious term. Many authors treat ‘culture’ and ‘tradition’ as essentially synonyms, but others, often mindful of how much more complex human culture is than anything encountered in other species, suggest we gain more insight by requiring additional criteria for culture, such as being based on imitation and teaching (Galef, 1992) or involving multiple and diverse traditions (Whiten and van Schaik, 2007), features thought to be particularly distinctive in human culture.

We relate discoveries about primate social learning and culture to neuroscience in two main ways. First, at a relatively ‘macro’ level we review evidence that the size of the brain or major parts of it are associated with an emphasis on the extent or nature of social learning in the species concerned. This perspective invokes what has accordingly been called the ‘cultural intelligence hypothesis’ (Whiten and van Schaik, 2011). This in turn can be considered a special case of the ‘social intellect’ (Whiten and Byrne, 1988a) or ‘social brain’ (Dunbar, 1998) hypotheses to explain primate intelligence, so

we begin our review with a brief overview of these ideas and the evidence bearing on them, relevant for the overarching topic of ‘social cognition’ in this journal theme issue. At a second, more ‘micro’ level we note the relevance of discoveries about the scope of imitative matching and learning in primates to the operation of mirror neurons, that fire both when an animal executes a certain action or observes it performed by others. This discussion begins with non-human primates, in which mirror neurons were first discovered (Rizzolatti et al., 2001), but extends importantly to humans, in which associations with imitation were first identified (Iacoboni et al., 2001; see Molenberghs et al., 2009, Iacoboni, 2010, and Ferrari and Rizzolatti, for reviews) and where distortions in the mirror system have been hypothesized to be linked with autism (Williams et al. 2001).

2. Social intelligence and the ‘social brain’ of primates

Humphrey (1976) was the key originator of what came to be called the “the social intellect hypothesis”. The core of his proposition was that the acknowledged lively intelligence of non-human primates (henceforth ‘primates’) was not adapted so much for dealing with physical problems in domains such as foraging and avoiding predators, but instead reached its highest sophistication in grappling with the special complexity being discovered in primates’ social lives. Such ideas were prefigured by some earlier speculations about primate social complexity (e.g. Jolly, 1966) but Humphrey expressed the theory in an explicit and articulate fashion with major impacts on primatologists conducting empirical studies, who were beginning to record the social complexities he alluded to.

2.1 Social and Machiavellian intelligence hypotheses

Just over a decade later, sufficient empirical work on primate social cognition and complexity that included shifting alliances and coalitions (de Waal, 1982), social knowledge (Cheney et al., 1986) and tactical deception (Whiten and Byrne, 1988b) had accumulated, collated in the first integrative volume on the topic: *Machiavellian Intelligence* (Byrne & Whiten, 1988). The title echoed de Waal’s account of the

dynamic power manoeuvrings amongst chimpanzees (*Chimpanzee Politics*, 1982) which could quote the advice given by Nicolo Machiavelli (1531) about how politicians could socially manipulate their subjects, because it so well matched chimpanzees' tactics. Byrne and Whiten emphasized not only the devious social scheming for which Machiavelli has bequeathed his name to everyday language, but rather, the key mix of competitive *and cooperative* manoeuvres that Machiavelli identified. Management of such social tactics creates pressure for greater skill in others, in the potentially spiralling Machiavellian arms races that Humphrey first sketched. Humphrey (1976) compared primate social life to a game of chess, in which one's gambits were played out in a social arena where the other players are constantly reactive and responsive. This may create a selection pressure for increasingly nimble social tactics, that can be expected to evolve up to a ceiling of social cognition limited only by the economics of devoting sufficient neural and other resources to such functions (see Isler and van Schaik, 2014, on the 'expensive brain framework').

Whiten & Byrne (1988a) distinguished three levels of the social or 'Machiavellian' intellect hypothesis ('MIH'). The most basic is the hypothesis that in contrast to much early work that focused on intelligence in relation to physical problems typical of comparative psychologists' laboratories, primate intelligence in the wild is actively engaged with social life. This version of the hypothesis may appear elementary today, but has driven over two decades of ingenious research identifying the complexities of primate social cognition, in both wild and captive primates (Seyfarth & Cheney, 2015a,b, and papers in this journal issue).

The second and more ambitious version of the hypothesis proposes that intelligence has been moulded more by social life than by physical demands such as foraging and predator evasion. Version three goes further, to propose that the very nature and scope of intelligence has been shaped by these social selection presses, so that primates' brains and cognitive potentials have become specifically adapted for dealing with complexities characteristic only of the social realm. What Humphrey (1976) called 'natural psychology', later called 'Theory of Mind' or mindreading, offers a striking example, that stimulated productive empirical research with primates particularly in the present century (Call and Santos, 2012; Whiten, 2013; Krupenye et al. 2016; Meunier, this issue).

To many primatologists who in their research on primate social life have daily been impressed by its intricacies, these hypotheses may have an inherent plausibility, but testing them rigorously is challenging. One early approach to this was due to Dunbar (1995), who examined the relationship between measures of a primate species' relative brain size – encephalization – and the average size of social groups in the species, adopted as an initial, if very basic, measure of social complexity. Remarkably, despite the crudeness of both measures, Dunbar found the positive relationship between them that the second version of the MIH predicts (Fig. 1). Dunbar dubbed the neural version of the MIH supported by such discoveries the 'Social Brain Hypothesis' (Dunbar, 1998; and see Brothers (1990) for a pioneering exploration of the concept of a 'Social Brain'). The variables involved in such tests, group size and neural volumes, may be crude but are more amenable to straightforward measurement than either social complexity or the sophistication of social cognition. The tractability of the approach has generated a substantial corpus of studies further exploring these relationships, that we briefly review next.

< insert figure 1 about here >

2.2 Social complexity and encephalization: empirical tests

Although social complexity and degrees of encephalization are in principle subject to empirical measurement, this does not mean the process is straightforward. For example, larger animals tend to have larger brains, so such allometric relationships must be allowed for; and concerning social complexity, a meaningful social unit needs to be focused on, which is inherently challenging in fluid or hierarchically structured primate communities.

Controlling for body size has been addressed by controlling directly for this variable by regressing brain size first on body size and then considering residuals – but this is not straightforward because the effects are nonlinear. A variety of alternative approaches have been developed. For example, Dunbar (1998) measured the 'neocortex ratio', the ratio of neocortex volume to the volume of the remainder of the brain, and found this index to be positively correlated with a species' average group size. This was

not the case for other, ‘ecological variables’ like home range size, which would be expected if primate intellect has evolved for dealing with physical complexities such as navigation and foraging on a complex distribution of foods. Accordingly Dunbar’s results supported the social brain hypothesis. More refined measures of social complexity have also been explored, such as the size of the social ‘cliques’ that concern an individual’s most intense social relationships (Kudo & Dunbar, 2001), and the frequency of ‘tactical deception’ episodes reported in the research literature (Whiten & Byrne, 1988b; Byrne & Corp, 2004), with the predicted relationships with neocortex ratio again confirmed.

When such analyses have been extended to birds, it was not the size of social communities or social systems that explained relative brain size, but rather the mating system, with the greatest encephalization in those species with long-term pair bonding (Emery et al. 2007). Shultz and Dunbar (2007) further explored the sociality-encephalization relationship in carnivores, bats and ungulates as well as primates and found that pair-bonding was most strongly related to relative brain size in all of these taxa except primates. What might explain this? Emery and colleagues as well as Shultz and Dunbar shared the interpretation that in both birds and mammals, pair-bonding and the bi-parental care associated with it involve the management of intimate co-ordination and synchrony, which selects for encephalization. In primates it is suggested that analogous, bonded, and intricately negotiated relationships extend the same principles across larger social networks (Emery et al. 2007; Shultz & Dunbar, 2007). Shultz and Dunbar (2010) further showed that encephalization is most marked in those taxa of mammals with higher degrees of sociality, of which primates typically offer prime examples, supporting the social brain hypothesis from another perspective.

These broader taxonomic analyses suggest interesting implications for the evolution of the human ‘social brain’ (for reviews of this work, see Dunbar & Shultz, 2007, 2010). First, we humans are primates, so this body of research suggests that our sophisticated social brains did not emerge ‘out of the blue’, but instead have evolved on the back of socially-driven neural adaptations widespread amongst primates, implying an important shared pre-human ancestry. Second, we are unusual amongst the apes to have developed pair-bonding, found to be a modal characteristic of those hunter-gatherer societies that offer the best models for our evolutionary past ways of life

(Marlowe, 2005; Whiten and Erdal, 2012). In such societies, there is bi-parental investment because fathers invest in the development of their offspring in a variety of ways from food provisioning to education, for example in relation to hunting (Hewlett et al. 2011). These two features, the complex social life we share with other primates (and have made even more elaborate: Whiten and Erdal, 2012) and more unusual pair-bonded parental investment embedded within band life, may together help to explain the unique degree of encephalization that has tripled the brain size of our species in just over two million years. As we shall see below, these characteristics take on special significance in the realm of social learning and culture.

Of course, such effects of selection for social cognitive sophistication on primate brains have been enmeshed in a complex web of other factors. Such benefits are energetically costly, so can only evolve if they achieve payoffs that more than compensate for this, which in turn can be expected to be associated with adaptations to particular types of ecological niche and other factors such as life history variables. Such dynamics are beyond the scope of this review but have been explored in some depth for both non-human and human primates by Isler and van Schaik (2014).

Despite such complexities, further explorations of relationships between social complexity and brain variation in both human and non-human primates have extended to consider particular parts of the brain (Platt et al. 2016). In humans, for example, the size of peoples' social networks predicts the volume of regions such as the amygdala, implicated in emotional responses and vigilance (Bickart et al. 2011) as well as other parts involved in social functions such as the orbitofrontal cortex (Powell et al. 2012) and ventromedial prefrontal cortex (Lewis et al. 2011). Kanai et al. (2011) showed that the number of people's Facebook friends is correlated with the density of grey matter in the superior temporal sulcus (STS) and temporal gyrus.

3. Cultural intelligence and the 'cultural brain'

In more recent years a 'cultural intelligence hypothesis' (CIH) has been developed in part to address findings that the MIH does not explain well, notably the large absolute and relative brain sizes of the great apes, not all of which live recognizably complex social groups (van Schaik, 2006; Whiten and van Schaik, 2007; van Schaik and Burkart,

2011). However the CIH should apply to all species where cultural transmission becomes extensive and/or complex in nature.

The CIH can be regarded as in some respects a descendant or subsection of the MIH, and in some respects a competitor to it. It can correctly be thought of as a subsection insofar as it focuses on *social learning*, which provides one component of social complexity. Thus, Whiten and Byrne (1988a), in dissecting a suite of facets of ‘Machiavellian intelligence’ such as social knowledge and theory of mind, already included social learning and cultural transmission. Allusions to these dimensions of complexity in the social worlds of primates had in fact been made earlier in the foundational articles of Jolly (1966) and Humphrey (1976). As Whiten and van Schaik (2007) noted, the largest part of a major compilation of work under the title of ‘social complexity’ was already headed ‘cultural transmission’ (de Waal and Tyack, 2005). However, to properly explicate the CIH, we need first to offer an overview of what we have learned of the scope of culture in non-human primates.

3.1 *The scope of ‘culture’ in primates*

The study of potential cultural behaviours in wild primates has long been led by chimpanzee researchers, from Goodall (1986) through McGrew (1992) to Boesch and Tomasello (1996) charting accumulating evidence that, like people, chimpanzees behaved in different ways across their distribution in Africa, with circumstantial evidence such as youngsters’ intense peering at adult tool use indicating a cultural basis. The first systematic syntheses became possible when the leaders of nine long-term projects collaborated to agree behavioural definitions and pool their data (Whiten et al., 1999, 2001). Starting with 65 candidate behaviour patterns, 39 were identified as putative cultural variants (traditions) because they were common in at least one community yet absent in at least one other, with no apparent genetic or environmental explanations (such as being determined by the availability of key resources). This number of traditions was unprecedented in comparison to existing reports for other animals, that typically reported just one or a handful of such variants; moreover they spanned much of chimpanzees’ repertoires, with examples from tool use for foraging, comfort and hygiene purposes, grooming, communication and sexual behaviour. Each

community was found to exhibit a unique array of such variants so that a chimpanzees' behavioural profile could be sufficient to allocate it to the region in which it lived; a cultural 'quilt' diagram illustrating such patterning, after Whiten et al. (1999) is illustrated in electronic supplementary information in Figure S1 along with a later, more fine-grained one.

Although these findings did not discriminate between specific potential social learning mechanisms responsible, they nevertheless have profound implications for primate social cognition, because they imply that these apes live in a cognitive world that is shaped by the cultural variants of their parents or parental generation in a significantly rich way.

An extensive range of supplementary chimpanzee studies followed, illustrated by selected examples in Table 1, and other fieldworkers applied what came to be called the 'method of exclusion' (inferring cultural transmission where environmental and genetic explanations were judged implausible) to other species. Thus orangutans were reported to display over 20 (later, over 30) cultural variants (van Schaik et al. 2003; for follow up studies see Table 1), leading to the inference that this degree of cultural complexity would likely have characterized the common ancestor of all the great apes, around 14 million years ago (van Schaik et al. 2003; Whiten and van Schaik, 2007). Likewise, a consortium of gorilla researchers have recently produced a similar analysis reporting 23 different cultural variants (Robbins et al. 2006).

< Insert Table 1 about here >

Other primates have since been reported to sustain cultures constituted by multiple traditions of different kinds, notably spider and capuchin monkeys (Santorelli et al. 2011a; Perry et al. 2003; Table 1 and Figure S1 c). Interestingly, these species exploit ecological niches in the New World that share some commonalities with those favored by chimpanzees in the Old World, and they are also large-brained; spider monkeys have the largest brains amongst New World primates and capuchins have the highest encephalization quotient (brain size corrected for body size) of any monkey. Such features are consistent with the cultural intelligence hypothesis that we discuss next,

which proposes an adaptive linkage between encephalization and the complexity of cultural transmission on which a species relies.

However, we note that the number of species for which serious investigations on the scope of culture have been published remains regrettably small, as Table 1 demonstrates. This may be due in part to the demanding requirement for long-term studies of multiple groups of the same species, of which there are still all too few. This means that we must be correspondingly cautious about the significance of those species mentioned above, that are prominent in the table so far – an issue we return to in the section that follows.

3.2 The cultural intelligence hypothesis

Measures of encephalization and social complexity exhibit a good fit across primates as a whole, but the fit is better if the great apes are considered separately, because as a family they are even more encephalized (Fig. 1). This difference is not well explained by the social intellect/brain hypotheses, because aside from chimpanzees' distinctive fission-fusion communities, the apes cannot be claimed to exhibit greater social complexity. Noting the complexity of culture attributed to the great ape family on the basis of the chimpanzee and orangutan field data outlined above, van Schaik (2006) and Whiten and van Schaik (2007) developed a 'cultural intelligence hypothesis' (CIH), proposing that the complexity of culture may help explain the enlarged brains of the apes. Like the MIH, the CIH is not inherently restricted to primates but could apply to any animals that display these characteristics, so other potential candidates might include large-brained cetaceans that evidence cultural complexity, spanning both vocal and behavioural domains (Rendell and Whitehead 2001; Whitehead and Rendell 2015).

The CIH is in one sense a competitor to the MIH insofar as its potential to explain encephalization is concerned, but equally it can be seen as a particular version of the social intellect hypotheses, emphasizing one particular component of an animal's social life concerned with the transmission of culture. The CIH in turn embodies multiple strands. One is the proposition that 'culture makes you smart'; that what a child or juvenile primate acquires from its cultural heritage gives it a greater competence in varied but important aspects of its daily life, ultimately enhancing reproductive

potential. In turn, the importance of culture to the species concerned is expected to shape and enhance the cognitive underpinnings of key cultural processes, and thus the corresponding structures in the social/cultural brain. This includes multiple capacities for (i) cultural transmission such as imitation, emulation and teaching, (ii) storage of an expanding cultural repertoire, and (iii) the intermittent creation of the innovations that feed cultural change. The hypothesis that ‘culture makes you smart’ is thus proposed to operate both on ontogenetic-developmental timescales and on the long-term evolution of species’ brains and culture-related cognitive capacities (van Schaik and Burkart 2011).

Evidence supportive of these hypotheses comes from a variety of sources across humans, apes, other primates and non-primates, explored by Whiten and van Schaik (2007) and van Schaik and Burkart (2011). In humans, of course, the proposition that ‘culture makes you smart’ is uncontentious; indeed, it is the basis of our educational systems. For the non-human primates the hypothesis was originally developed to explain the particular enhanced encephalization of the great apes, and the evidence is arguably strongest for them. In chimpanzees, one particularly relevant study in the wild showed that juvenile females invested more time than did their male peers in closely observing their mother skilfully apply stem tools to extract prey from termite mounds (Lonsdorf et al. 2003). Most significantly, these females became ‘smarter’ in their mastery of the technique a whole year ahead of the males, also showing some matching to differences in mothers’ techniques (length of tool and depth of probing) than did the males. Such mastery is particularly important for females, who as adults spend more time in tool use for gaining invertebrate prey than males, who are able to gain more vertebrate prey through hunting (Whiten, 2006). More generally, most of the behaviour patterns in the corpus of putative chimpanzee traditions concern tool-aided or other forms of foraging technique. Becoming culturally competent in these techniques can significantly extend these animals’ lifetime success, as in helping them through dry-season bottlenecks in fruit availability, where technology has been shown to provide critical access to other food sources such as nuts and otherwise resistant embedded food sources not available to other species (Yamakoshi, 1998).

Orangutan culture also incorporates such life-skills. Forss et al. (2016) and Burkart et al. (2017) suggest that in a species that depends significantly on cultural transmission,

there will be correlated selection on individual intelligence. Forss et al. (2016) provide evidence in support of this insofar as Sumatran orangutans, which display a more extensive and complex cultural repertoire than their Bornean cousins, achieve more in zoo-based tests of ‘general intelligence’ and have marginally but significantly larger (by 2-12%) brains.

Experimental studies complement and reinforce these findings from the field (Whiten, 2015). Multiple studies show that chimpanzee tool use is socially learned, through both dyadic experiments involving a single model and single observer (Whiten et al., 2004) and diffusion experiments in which different forms of tool use, seeded in different groups, pass from individual to individual, creating incipient traditions that deliver access to a food source otherwise unavailable (Whiten et al., 2007). Relevant examples of each are that East African chimpanzees who do not nut-crack in the wild learned to do so through observation of a skilled nutcracker (Marshall-Pescini & Whiten, 2008a); and that alternative forms of stick-tool use to solve an artificial foraging task spread further in the groups into which they were seeded (Whiten et al., 2005).

A different kind of evidence supporting the CIH is that for both chimpanzees and orangutans, Whiten & van Schaik (2007) showed that greater opportunities to learn from others, deriving from more extended times in association with groupmates in some communities, predicted the acquisition of the more complex techniques of each ape’s cultures. In a more fine-grained study, Schuppli et al. (2016) recorded the intense ‘peering’ behaviour of wild juvenile orangutans, finding its occurrence confirmed a suite of predictions concerning its role in skill acquisition, such as that relevant exploration was enhanced following close peering events of events like nest-building and tool use. A further, complementary kind of evidence is that the ‘enculturation’ of young apes raised in intimate relationships with human culture tends to create an enhanced capacity to learn by imitation and a corresponding repertoire of competences in aspects of the surrounding culture, from symbolic communication to use of artefacts ranging from cups to toothbrushes (Tomasello et al. 1993a; Tomasello and Call, 2004; Whiten, 2011).

The sophistication of social learning in the apes is also relevant and further reviewed in the following section. As noted above, the findings indicated in Table 1

together with their encephalization status suggests that both capuchins and spider monkeys may also fit the predictions of the CIH, even if the linkages are less robust for them. Supplementary experimental evidence is more lacking for these monkeys, but for capuchins at least, there is some evidence of social learning effects strong enough to sustain laboratory traditions (Dindo et al. 2008, 2009), and evidence for selective attention to the most proficient nut-cracking adult models has been documented in free-ranging capuchins (Ottoni et al. 2005). By contrast we are not aware of any such experimental studies of social learning in spider monkeys, and the survival value of many of the cultural variants identified in the wild for this species (Santorelli et al. 2011a) beg further study.

More broadly based evidence that social transmission is associated with enhanced cognition comes from a study that identified correlations between a measure of encephalization ('executive brain ratio' – the volume of the cortex plus striatum, relative to brain stem) and the prevalence of social learning in a species, based on reports in the research literature (Reader & Laland, 2002). Social learning explained more of the variance than any of the other variables analysed in this study, with an r^2 of 0.48 (Fig. 2). Reader and Laland (p. 4440) concluded their results "suggest an alternative social intelligence hypothesis to those stressing the Machiavellian characteristics of mind-reading, manipulation and deception"; instead, "individuals capable of inventing new solutions to ecological challenges, or exploiting the discoveries or inventions of others, may have had a selective advantage over less able conspecifics, which generated selection for those brain regions that facilitate complex technical and social behaviour".

< insert figure 2 about here >

This conclusion is clearly consistent with the cultural intellect/brain hypothesis. However, research particularly by Barton (2006; Barton and Harvey, 2000) has shown that many brain components coevolve as a network, so that more recent studies of this kind have tended to retreat to examining cognitive correlations with absolute brain size, or total brain size corrected for body size (see also Deaner et al., 2006). The most recent study in this line (Navarrete et al., 2016) was focused on primate innovation and tool

use, but also included the measure of social learning frequency employed by Reader and Laland (2002); it confirmed and extended their findings, concluding from the relationships between them that encephalization and capacities for both innovation, especially innovation involving tool use, and social learning coevolved. Inference of any simple directional causality between these cannot be established - most probably they influenced each other over their evolutionary history. Nevertheless, Navarrete et al. (2016) suggest that one plausible interpretation of their findings is that “through social transmission many primates learn to exploit novel foods, and the resources so gained both aid survival and fuel brain growth” (p. 8). Moreover, in relation to the discussion of social intelligence further above, these authors note that the consistent linkage they find between “social group size and brain size support the established finding that social intelligence is an important driver of brain evolution” (p. 8).

Nevertheless, caution seems in order in relation to social learning in these studies, for the data used were simply those reported in the primate literature. They may thus be subject to several forms of bias, such as that certain researchers interested in topics like intelligence and culture selectively target what they anticipate are promising species, and these researchers may then be more likely to be motivated to put observations of corresponding behaviour into print for these species. Lefebvre (2013) discusses a variety of potential biases of this kind and how corrective measures may be implemented.

An intriguing complication in the picture is the discovery by Barton and Venditti (2014) that it is the cerebellum that has expanded fastest in the great ape family, a trend carried further in humans. It has been common to focus on the neocortex as the seat of ape, and particularly human intelligence, no less so than for social intelligence, yet as Barton and Venditti point out, the human cerebellum contains four times as many neurons as the neocortex and it has expanded at several times the rate of the neocortex amongst the apes. These authors calculate that as a result, in human evolution approximately 16 billion more cerebellar neurons have been added beyond expectations for our brain size, equivalent to all the neurons in the neocortex! Yet the cerebellum is the relative ‘Cinderella’ of the pair (in fMRI work, it is often even omitted from the image!) and its functions are less well understood. Barton and Venditti suggest that key functions in relation to their analysis are likely to include “learning of sensory-motor

skills, imitation, and production of complex sequences of behaviours” (p. 2442) and the cerebellum is in any case massively inter-connected with the neocortex.

3.3 ‘Vygotskian’ and ‘cultural intelligence’ hypotheses

The cultural inheritance hypothesis discussed above was developed to explain variance amongst non-human primates, and great ape encephalization and social learning in particular. It is important to recognize that Moll and Tomasello (2007) instead offered a potentially complementary, human-focused ‘Vygotskian intelligence hypothesis’, proposing that “primate cognition in general was driven mainly by social competition, but beyond that the unique aspects of human cognition were driven by, or even constituted by, social cooperation” and that “regular participation in cooperative, cultural interactions during ontogeny leads children to construct uniquely powerful forms of perspectival cognitive representation”. (p. 639). Lev Vygotsky’s name was an appropriate one to adopt for this, given his classic writings on culture and collaboration in cognitive development, and the hypothesis nicely complemented the broader CIH that Whiten and van Schaik contributed in the same themed journal issue (“Social intelligence: from brain to culture”; Emery et al. 2007). However, in presenting data supportive of these ideas from comparisons between children and other apes in social versus physical cognition, an article by Herrmann et al. (2007) now referred to the Vygotskian version as the “cultural intelligence hypothesis” - a potentially confusing step because this hypothesis, seeking to explain ape/human differences, has a different focus to the CIH which is about differences across primates and even broader classes of animal. Accordingly we advocate that either there be a reversion to the label of ‘Vygotskian intelligence hypothesis’ to mark the specific scope explicated by Moll and Tomasello, or alternatively the two hypotheses may be harmonized with each other, each essentially representing different points along a continuum of complexities in cultural cognition on the one hand, and encephalization on the other. We advocate exploring the latter as an interesting option for future development.

4. Social learning, brain circuits and the mirror neuron system

Primate social learning has been studied for over a century (Whiten and Ham, 1992; Tomasello and Call, 1997) and has been yet more intensely researched in recent decades (Whiten, 2012). Much of this work in the last century focused on the question of what kinds of social learning processes were at work, but in recent years new perspectives have emerged. Notable amongst these has been an extension of experimental designs beyond the common ‘what does primate B learn from primate A?’ to social diffusion experiments in which the spread of socially learned information is tracked across and between groups, linking more directly with research on primate cultures at large, outlined above. A further new focus has been on adaptive, contextual selectivity in social learning, for example in relation to preferential learning from certain classes of individual, such as those most skilled (Price et al. 2017; Watson et al. in press). As a result, we now know an enormous amount about social learning in a widening array of primates, less about the enormously complex underlying neuroscience of such learning. Further below we focus on potential links between aspects of our findings in primate social learning and some new discoveries about relevant neural circuits and the functioning of what has come to be called the mirror neuron system.

4.1 Primate social learning: imitation, emulation and cultural diffusion

As animal social learning theory has developed, increasingly complex taxonomies dissecting the diverse psychological processes involved have been developed (Whiten et al. 2004; Hoppitt and Laland, 2008). However, three broad categories have dominated this research area: imitation, emulation and stimulus/local enhancement.

The distinction between emulation and imitation emerged when, in a study of chimpanzees’ social learning of using a rake to acquire food, Tomasello et al. (1987) observed that, although most chimpanzees did not copy the particular motor act a model used to acquire food, they did apply the tool more successfully than could be accounted for by mere ‘stimulus enhancement’, in which social learning involves only the drawing of attention to a particular object. Tomasello et al. suggested that the chimpanzees had observed “the relation between the tool and the goal” (p. 182) and learned “to use the tool in its function as a tool” (p.182), a type of social learning that Tomasello (1990) later labelled ‘emulation’. Tomasello noted that in emulation the observer may act “in

any way it may devise” (p. 284) to achieve the goal or result it had seen attained, thus contrasting with imitation, which is defined by matching to the actions of the model observed. Accordingly, to a first approximation, imitation is copying the actions of another individual, whereas emulation is copying only the results the model achieves.

A series of experiments comparing children’s social learning with that of chimpanzees and focused on emulation followed. In the first, children copied a human model’s trick of flipping over a pronged rake to pull in a reward and were described as imitating, unlike chimpanzees who used the tool without replicating the flip action and were therefore described as emulating (Nagell et al. 1993). Call and Tomasello (1994) found similar copying in orangutans. On the basis of such studies, Tomasello, Kruger et al. (1993a) argued that the earlier assumption that chimpanzees (and other primates) were capable of imitation was not supported; instead, they emulate, and the only true imitators are humans, who display high fidelity copying in childhood. The case for this dichotomy between non-human primate emulation and human imitation has been supported by a growing set of studies over the years, and hypothesized to be key in explaining the gulf between the richness of human culture and particularly its cumulative nature, contrasting with the limited cultures of other primates (Tomasello et al. 1993a; Tennie et al. 2009).

However, results have also emerged in our own studies and those of others that indicate a measure of imitative capacity in both apes and monkeys. We review these studies below and suggest their relevance to the function of mirror neurons. Mirror neurons are a class of neurons identified in the premotor cortex of macaque monkeys, that fire not only when the monkey performs a certain action such as grasping a food item, but also when it sees another monkey do this (Rizzolatti and Fogassi, 2014). In discussing the potential function of these neurons in primates, the researchers involved initially dismissed what might seem the most obvious – imitation – because they did not see evidence of imitation in their monkeys and they noted a current scepticism about the occurrence of imitation in monkeys generally, as noted above (see also Visalberghi and Frigaszy, 2002). Instead they proposed that the function of these neurons was in effect to ‘stand in the shoes of the other’ and through this mirroring, recognize the goals inherent in the actions of others (Rizzolatti et al. 1996; Gallese and Goldman, 1998).

Our results concerning bodily imitation in monkeys and apes, reviewed further below, moderate this view that non-human primates lack the capacity for matching and replicating the actions of others apparent in human imitation. However there is another set of studies to which we draw attention, that demonstrate matching and replication on a scale relevant to the larger question of cultural transmission. These are cultural ‘diffusion experiments’, that go beyond the classic, dyadic ‘does B copy A?’ design of most 20th century research, instead tracking the outcome of an initial seeding of a novel behaviour as it spreads (or not), across multiple individuals. By 2008, Whiten and Mesoudi were able to review 33 such studies in animals, including 17 on primates. Whiten et al. (2016) have reviewed 30 further diffusion studies published since, of which as many as 20 were on primates and these are summarized in Table 2. The resilience of replication shown in these studies is very variable, which in itself is consistent with the relatively negative conclusions drawn about primates’ powers of copying outlined above. However, this corpus of studies includes some that do show considerable resilience. For example amongst the ape studies, Whiten et al. (2007) found that alternative foraging techniques (both with tool-use, and not) seeded in separate groups of chimpanzees spread with significant fidelity across these groups, and then to a second group who watched the first one, and in the same way to a third. Interestingly, some ‘corruption’ that occurred along the way, in which a few individuals discovered the technique used by the other group, were over-ridden such that the third group expressed good conformity to the technique originally seeded in the first group. Amongst the monkey studies we find a similar phenomenon, as alternative seeded foraging techniques spread across two groups of capuchin monkeys, showing occasional corruptions but nevertheless maintaining resilience of the alternative incipient traditions (Fig. 3; Dindo et al. 2009).

< insert figure 3 about here >

We highlight these studies here to emphasize that non-human primate social learning can be capable of significant copying fidelity, sufficiently potent to sustain alternative traditions. However such effects can also be fragile, with several studies in Table 2 reporting weak fidelity. Moreover, these studies do not discriminate whether

fidelity is maintained by imitation of the actions involved, or emulation of the results of actions (e.g. in Fig. 3, door rises versus door slides). This is an issue we consider in the two sections to follow and is a significant issue in the neuroscientific analyses of Hecht et al. (2013a,b) we shall discuss there.

4.2 Forms of social learning in apes and monkeys; neural circuits and mirror neurons

Much more research on social learning has been undertaken with chimpanzees and other apes than with any species of monkey, and several of the methodological approaches have not been replicated for both monkeys and apes, so here we discuss apes (principally chimpanzees) first, and monkeys separately.

4.2.1 Imitation, emulation and the scope of social learning in apes

Soon after setting out the basic ‘chimpanzee-emulators versus child imitators’ hypothesis, Tomasello and colleagues provided one particular exception. Savage-Rumbaugh had remarked that chimpanzees and bonobos participating in her explorations of language-like abilities, which involved highly enriched learning contexts, displayed spontaneous imitation; accordingly, Tomasello, Savage-Rumbaugh et al. (1993b) conducted a battery of formal tests inviting the apes to copy a wide range of novel actions on objects, such as squeezing the bristles on a brush, or instead using it to paint some foam on the floor. Three chimpanzees with the most intense ‘enculturation’ into human daily life displayed recognizable imitation in nearly half these cases, as did two year old children tested similarly, whereas other, mother-reared chimpanzees showed very little. Thus, here was evidence both that quite high fidelity copying is within the grasp of at least some non-human apes; and (ii) that it is significantly enhanced during development by an appropriate social environment. We suggest it is unlikely the latter conjures imitative ability out of the blue.

In this 1993 study chimpanzees were verbally invited to “Do what I do”, an approach that shared some methodological overlap with an earlier study by Hayes and Hayes (1952) in which a home-raised chimpanzee was first trained to imitate a series of actions on the invitation to “Do this”, then tested on a battery of more novel actions, many of which the chimp, Viki, was reported to copy. The basic approach was replicated by Custance et al. (1995) with two young non-enculturated chimpanzees,

with the important added rigor of responses being classified by coders blind to what action the chimpanzee had seen. This was also replicated by Call (2001) with an enculturated orangutan. In both studies response matches to each of the 48 test items could be identified at significant levels by the coders. The orangutan was reported to fully imitate 58% and partially imitate another 36% of the target items.

Such studies are important in relation to those definitions of imitation in which some authors require bodily matching between what the model does and what the observer does, to discriminate imitation of actions from emulation. All the target items of Tomasello et al. (1993b) employed objects, so it is difficult to rule out the possibility that the chimpanzees were replicating what the objects did, rather than actions of the model. By contrast the battery employed by both Custance et al. and Call included many purely bodily actions, including whole body ones like hugging oneself, and finer facial and manual actions, like ‘clap back of hand’. These studies thus demonstrate a mapping in these apes of body-part, model-to-self correspondence, a finding that is further complemented by a study by Buttelmann et al. (2007) in which chimpanzees copied some bizarre uses of body parts such as a head touch to switch on a light.

Such bodily correspondence is what is coded in the firing of certain mirror neurons identified in the research program of Rizzolatti and colleagues cited above. Mirror neurons were discovered in, and have principally been further studied in, macaque monkeys rather than apes, but brain imaging with humans has identified regions homologous to those where mirror neurons are recorded in monkeys, that respond to observed actions of others in similar ways, and the network of these regions is referred to as the ‘mirror system’. Accordingly it is likely that mirror neurons are to be found in other primates including apes (indeed, mirror neurons for vocalization have also been reported in songbirds, that typically learn their song by copying others: Mooney, 2014). Moreover, through further fMRI studies, the human mirror system has been implicated in imitation, among other functions (Iacoboni et al. 2001; Iacoboni, 2012; Rizzolatti et al. 2001). Putting all these findings together, the demonstration of significant bodily imitation in chimpanzees now makes it a plausible hypothesis that mirror neurons support imitative functions in our closest ape relatives, that are capable of the degree of matching shown in the Custance et al. and Call studies.

One fine-grained analysis within a chimpanzee social learning study appears particularly relevant to this likelihood. In a study of the social learning of nut-cracking in East-African chimpanzees, Marshall-Pescini and Whiten (2008b) reported that when naïve young recruits watched an older, skilled nut-cracking model, they would sometimes show some entrainment (even synchrony) of downward striking actions like those of the hammering model. This cannot be emulation because the recruit is holding no hammer stone and has no nut – it is pure bodily mimicry. Fuhrmann et al. (2014) have since analysed the relevant video records frame by frame, as shown in Fig. 4 (and see video clips in the electronic supplements to these two papers), allowing sophisticated time-series analyses to objectively confirm significant motor matching and entrainment, even though such phenomena appeared to repeatedly ‘spill over’ in the actions of only one youngster in particular. This kind of entrainment, linking visual perceptions of another’s actions with motor correspondences in oneself, is just the kind of linkage that is signalled by the firing of mirror neurons.

< insert figure 4 about here >

The same can be said for the reverse process of recognizing when another individual is imitating one’s own actions, which was first demonstrated in an experiment by Nielsen et al. (2005). In this study, after a period in which humans copied the spontaneous actions of a chimpanzee, the ape started to vary its actions with apparent intent, monitoring the imitative efforts of the human, and did so more than in a series of control conditions such as contingent but non-imitative responses. More recent studies have replicated the phenomenon, reporting it to be elicited by the imitative actions of a humanoid robot (Davilla-Ross et al., 2014) and to be correlated with variation in other social and communicative competencies (Pope et al., 2015). Such imitation recognition calls on neural mechanisms that code the correspondence between another’s actions and one’s own, just as the primary process of imitation does.

However, we note that bodily matching is not the only way imitation has been defined. Byrne and Russon (1998), in an influential theoretical analysis, suggested that alternatively one might see imitation in the overall sequential or hierarchical structure of complex actions like nut-cracking, a phenomenon they called program-level imitation.

Accordingly, Whiten (1998) demonstrated that chimpanzees a convergence, over a series of trials, on whichever of two alternative sequences of disabling defences of an ‘artificial fruit’ they witnessed a model perform. An experiment by Horner and Whiten (2005) was in line with such conceptions but explored imitation versus emulation conceptualized as different ends of a continuum. In this study, when participant juvenile chimpanzees witnessed a model perform a sequence of tool-based actions on an opaque foraging task, it was predicted that a more complete imitative copy of the sequence would be seen than when the same task was transparent and the first segment of the action sequence could be seen to be causally unnecessary. This prediction was confirmed in the case of the chimpanzees, who thus produced a more ‘emulative’ response in the transparency condition. Surprisingly, in this study young children copied all segments of the sequence even in the transparent condition where causal irrelevance appeared visibly obvious, a disposition later dubbed ‘over-imitation’ (Lyons et al., 2007). Such over-imitation has since become a vigorous field of research particularly in developmental psychology (Whiten et al. 2009; Nielsen et al., 2014).

A different way in which the emulation/imitation distinction has been approached is via a ‘ghost experiment’ in which there is no model visible to imitate, and all an observer can watch is the movement of the objects normally caused by a model. This can be achieved in various ways, such as mechanically or by appropriate video manipulation. Hopper et al. (2007, 2015) found that chimpanzees learned nothing from such scenarios in a complex tool use task; instead chimpanzees seem to need to see another chimpanzee acting on the objects, implicating at least some basic level of imitation. However, in a much simpler task Hopper et al. (2008) did find evidence for emulation in a ghost condition. Tennie et al. (2010) went further, showing that when chimpanzees could not copy how they saw a human pour water into a tube to make a desirable peanut float up to be grasped, because the chimpanzees did not have the bottle the human had used, some chimpanzees collected water from their drinker and spat it into the tube instead – an impressive display of imaginative emulation!

Taking account of this array of findings and others, Whiten et al. (2009) rejected the simple dichotomy of emulating apes versus imitative children, and instead concluded that all these species have a ‘portfolio’ of social learning processes that include imitative, emulative and other, simpler forms, applying these in often adaptive

ways, selectivity according to context. Such selectivity may take a variety of forms; one has already been outlined in the differential response of young chimpanzees to the transparent and opaque test boxes of Horner and Whiten (2005). Other forms include choices between alternative models to copy, such as ‘copy the most successful’ (Watson et al. in press; Price et al. 2017).

Another form of selectivity is to copy the majority, thus potentially benefitting from what many of one’s groupmates have found to be a preferred option to choose. Whiten et al. (2005) found evidence suggesting conformity to the majority in a diffusion experiment in which alternative tool-use techniques were seeded in two groups and spread further in them, creating incipient traditions. Several individuals subsequently discovered the technique used by the other group, but by two months later they tended to have converged again on the technique favoured in their own group. However, this was a post-hoc finding and not one explicitly tested by an experiment. This was done by Haun et al. (2012), who showed that chimpanzees preferred to copy the choices of three chimpanzees over a single one, demonstrating a ‘copy the majority’ rule of conformity. Results consistent with this have been reported from the wild by Luncz and Boesch (2012, 2014), who discovered different preferences for seasonal nut-cracking tools in neighbouring communities and that females, who transfer between communities, came to display the same preference as residents, implying that these immigrants conform to the local norms they experience after transferring communities. The phenomenon of conformity has become a topic of much interest, and also contention, in the field of animal social learning (Claidière and Whiten, 2012; van Leeuwen and Haun, 2014; van Leeuwen et al., 2016; Whiten and van de Waal, 2016.).

As will be apparent, the research literature on ape social learning has become huge, particularly for our closest living relative, the chimpanzee, and we have been forced to be highly selective in the above review. Topics not covered here for want of space include so-called ‘rational’ imitation (Buttelmann et al. 2007), the selective copying of intentional acts (Tomasello and Carpenter, 2005), teaching (Hoppitt et al. 2008) and cumulative culture (Dean et al. 2012). For complementary reviews that address these and other current issues in this area, readers may wish to consult Whiten and Erdal (2012), Galef and Whiten (2017), Whiten (2017, a, b) and Watson et al. (in press) as appropriate.

4.2.2 Imitation, emulation and the scope of social learning in monkeys

Several of the complementary approaches to imitation that have been brought to bear on apes are not available for monkeys. For example, efforts to train monkeys to ‘Do-as-I-do’ have met with no success (Mitchell and Anderson, 1993; Frigaszy, Deputte et al. unpublished, cited in Visalberghi and Frigaszy, 2002). This in itself suggests an intriguing difference between apes and monkeys, with the former appearing to be able to recognize the act of imitation itself, unlike the monkeys tested. To our knowledge, episodes of model-observer ‘entrainment’ like that outlined above for nut-cracking chimpanzees have also not been recorded in monkeys, and equivalent ‘ghost experiments’ have not been completed (although see further below for a novel variant employed by Subiaul et al., 2004). These contrasts suggest a lesser facility in imitation in monkeys compared to apes, and it is not uncommon for authors to state baldly that monkeys do not imitate (Visalberghi and Frigaszy, 2002).

Limited evidence for bodily imitation has nevertheless been published, employing an approach applied in avian studies, where observer birds who witnessed a model stepping on a treadle to obtain food as opposed to a model using their beak to depress the treadle, showed a significant tendency to use the same body part (Zentall et al., 1996). Similarly, in a study of marmoset social learning of how to open a lidded food canister, those who watched a model using their hand to do so, as opposed to a model using their mouth, likewise showed a significant degree of using the same body part they had witnessed (Voelkl and Huber, 2000). This cannot be emulation because the result is the same in both cases: what is different is the action, which is what must be being replicated. The same authors later took a different approach to the question of imitation in their marmosets, performing a painstaking frame-by-frame analysis of the trajectory of a socially learned action that demonstrated a precision of matching to the model witnessed that departed significantly from chance (Voelkl and Huber, 2007).

Echoing the first marmoset study, van de Waal and Whiten (2012) offered similar food canisters with lids that could be popped off (‘aethipops’) to four groups of vervet monkeys in African sanctuaries. Most models and indeed most monkeys used their mouth to remove the lid, but in one group a model used her hands, and this method then spread significantly in her group (Fig. 5). Similarly in one group an individual grasped

the cords at the ends of the aethipop and pulled it apart like a Christmas cracker, a different approach that again spread significantly in this monkey's group. As in the studies summarized above, differential matching of body parts cannot be explained by emulation but only by action imitation.

< insert figure 5 about here >

Such cases of matching are again consistent with the operation of mirror neurons, as is complementary evidence that monkeys may recognize when another individual - even a human - is copying them (Paukner et al., 2005). Paukner et al. (2009) showed the macaques who were imitated looked longer at the person than in non-imitative control conditions, and moreover, were more prepared to engage in social interaction (object exchanges) with the person. Accordingly, putting these studies alongside those in apes summarized above, we propose that it was premature to demote imitative learning as an important potential function supported by this neuronal system in primates.

As was also the case for the ape research reviewed above, bodily imitation is far from the only topic being actively tackled with respect to social learning in other primates. An extensive range of studies has demonstrated social learning and cultural transmission in several species of monkeys and lemurs, even where these do not necessarily discriminate whether imitation or other processes are responsible. Several are included in the recent illustrations of diffusion experiments listed in Table 2 and others are reviewed by Subiaul (2007) and Whiten (2012). An innovative approach with macaque monkeys was described by Subiaul et al. (2004), in which a model received a reward after touching a series of images on a screen in a particular sequence independent of their (changing) locations in an array, while an observer monkey watched. The observer monkey was then later shown to learn such sequences faster themselves, implicating observational learning. Merely seeing the sequence occur without monkey actions, a kind of ghost condition, did not have the same effect. Subiaul et al. called the monkeys' achievement 'cognitive imitation', to stress that this is a form of copying what others do that unlike in most studies in this area, does not involve the acquisition of a manipulative skill. However, we think the term rather unfortunate

insofar as it may imply that instances of skill learning are not cognitive, which seems misleading.

< insert Table 2 about here >

A different kind of evidence for imitation concerns neonates. Meltzoff and Moore (1983) reported that human new-borns showed evidence of mimicking facial movements, discriminating tongue protrusion from mouth opening, for example. Meltzoff (2005) later linked the primordial bodily mapping implicated in neonatal imitation to the mirror neuron system, proposing both nativist and developmental elements. This work has been controversial, both with respect to whether such an infantile imitative capacity truly exists, and its relationship to later undisputed imitative competences (Oostenbroek et al., 2013, 2016), topics beyond the scope of this review. However, more surprisingly given the earlier, widespread dismissal of imitation in monkeys noted above, evidence for neonatal imitation in macaque monkeys has been offered by Ferrari and colleagues and again linked to the mirror system (Simpson et al., 2014). However, the suite of publications reporting these findings emanate from one research group and remain to be replicated by others, so that given the controversial nature of the parallel human neonatal imitation evidence, we highlight these results as providing a convergent source of evidence on imitation in monkeys, but remain cautious about interpreting them further.

Selectivity in monkeys' social learning has been shown in a number of studies. As for apes, these include biases about whom to learn from. Here questions shift from the cognitive abilities underlying different capacities for social learning to what motivates individuals to learn. De Waal (2001) conceptualised the latter in terms of what he called Bonding and Identification-based Observational Learning (BIOL), a motivation to be like others, such as one's mother or peers, as opposed to being dependent on physical rewards to copying, such as gaining food items. An example comes from the vervet monkeys we study, where we have identified an initial bias to learn from one's mother (van de Waal et al. 2013a, 2014). In the latter study this was revealed when the monkeys were supplied with sandy grapes, that mothers cleaned using one or more of several alternative techniques, which tended then to be adopted by their infants. Seeding

alternative ways to open an artificial fruit in different groups either in a sanctuary (van de Waal 2013b) or in the wild (van de Waal et al. 2010, 2015) demonstrated the spread of these alternatives via social learning, but the 2010 study revealed that this occurred only if the model was an adult female, not a male. This could make adaptive sense because females are the philopatric sex and are thus likely to provide the better models to copy than the males, who have immigrated into the group at some point and so have less experience about the optimal ways to behave in the local conditions pertaining.

Such migrant males, however, have provided evidence of conformity to majority preferences. In a study originally designed to examine the relative roles of social and individual learning in infants, two containers offering pink versus blue coloured corn were provisioned monthly, one made highly distasteful by soaking along with aloe leaves (van de Waal et al. 2013a). Two groups were in this way trained to avoid pink and two blue, while a new cohort of infants were suckling and taking no solid food. Several months later, when the corn options were offered again with no distasteful additive, adults maintained their bias and it was found that infants acquired this socially, adopting the preferences of their mothers and her group. Fortunately, in their migrations from pink to blue preference groups or vice versa, adult males provided a different class of individuals naïve to the local colour norm. Surprisingly, after watching the local monkeys eating, as many as nine of these ten males switched preferences already in their first choices, once they were not outranked by residents and could freely choose, demonstrating a remarkable degree of conformity. A different kind of evidence for the potential potency of social learning was offered by Perry (2009), who showed that despite young white-faced capuchins' experience with two alternative ways to open a difficult fruit, they eventually tended to settle on the one they had witnessed most.

4.2.3 Neural circuits, mirror neurons and social learning in primates

By contrast with all that has been learned about social learning and cultural transmission in many species of primate over the last century, neuroscience is only in the early stages of beginning to address these phenomena. Neuroscience, including that focused on mirror neurons, has tended to dismiss monkeys as simply not imitating. In part this may reflect the dispositions of the macaque monkeys studied in the neuroscience laboratories

concerned, and in part a limited reading of the literature. As reviewed above, there are reports of imitation in monkeys, that have perhaps not yet come to the attention of many neuroscientists. Similarly for apes, neuroscientists often cite conclusions from research groups who argue that apes emulate rather than imitating (Tennie et al. 2009), and in any case apes have been spared invasive neuroscience such as the single unit recording that identified mirror neurons.

However, some recent neuroscientific investigations have begun to interdigitate in interesting ways with the findings of comparative psychology concerning social learning. Hecht et al. (2013b) used positron emission tomography (PET) functional neuroimaging to record regions showing overlapping ‘mirror’ activation in relation to ‘transitive’ actions defined by having an object as their target, in both humans and chimpanzees, the latter being understudied in this respect, as we noted earlier. As predicted, such activation was recorded in chimpanzees in a distributed front-oparietal network homologous with that identified in earlier studies of the mirror systems of both macaque monkeys and humans. However whereas macaques characteristically show mirror responses *only* to goal-oriented, object-directed (transitive) actions (Rizzolatti et al. 1996), chimpanzees were found to resemble humans in also showing activation to transitive actions; indeed, transitive and intransitive activations were similar across regions homologous with those in which mirror neurons have been recorded in macaques.

Accordingly, the authors propose that the striking pattern of similarities and differences they report “suggests that chimpanzees map not only the results but also the movements of observed actions to the same brain regions that produce those actions. This may be a correlate of, and a prerequisite to, the ability to copy specific movements.” (Hecht et al. 2013b, p. 14129). This discovery appears entirely consistent with the conclusion of our review above, that chimpanzees are not limited only to emulative learning about the results of their actions, but also have in their social learning ‘portfolio’ an imitative capacity. These neuroscientific results are consistent with and may help explain the capacity of chimpanzees to learn, and show some facility in, ‘Do-as-I-do’ games, which are largely based on a battery of intransitive actions like ‘grab thumb’ (Table S1 in supplementary information) (Whiten and Custance, 1996), as well as monkeys’ repeated failure to master this game (Whiten et al., 2004). Nor are the

results inconsistent with our conclusions above concerning evidence of imitation in monkeys, because this derived from transitive actions on object where there was match to what was observed (e.g. oral versus manual foraging actions).

Complementary convergences between neuroscience and our behavioural findings also emerged through a related study by Hecht et al. (2013a) which applied the technique of diffusion tensor imaging to trace neural connections within mirror networks in macaques, chimpanzees and humans. The principal result of most interest in the present context concerns contrasts between ventral and dorsal streams of visual information processing, the existence of which have been important topics in neuropsychology for some time (see Milner and Goodale, 2008, for a recent ‘re-view’). In the present context the important findings were that on the one hand, a ventral stream was found to be robust in all three species, indicating a route of information between temporal areas (superior temporal sulcus) initially processing biological motion, inferior temporal cortex processing objects (that may include tools) and frontal areas processing actions goals. The authors suggest this stream will support extraction of action end-results or goals, the focus of emulative responses shown by all these species. However, dorsal streams contrast with the ventral streams along a continuum, being most robust in humans and least so in the macaques, with chimpanzees showing an intermediate state of development. Since these dorsal streams from temporal sensory areas to frontal areas link in inferior parietal cortex that is involved in the more fine-grained mapping of movements, the authors suggest this corresponds to the continuum from monkey to chimpanzee to human in their facility in discriminating and copying finer motor patterns. The authors’ schematic interpretation of these findings is illustrated in figure 6, which also indicates both (i) connections between parietal mirror regions and inferior temporal cortex, important in processing of tool characteristics, that are stronger in the tool-using chimpanzees than the monkeys, and yet stronger in humans; and (ii) connections between frontal and parietal regions extended further into superior parietal cortex in humans, an area associated with spatial awareness and attention. The authors speculate that the latter may support enhanced awareness of the trajectories of other’s actions, and these areas are activated during re-creation of humans’ early lithic tool-making (Stout et al. 2008; Hecht et al. 2015; and see Frey (2007) and Arbib (2010) for

further exploration of dorsal and ventral streams in relation to tool use, tool making and language).

The mirror system may encode others' actions in the frame of one's own motor system, but this also requires that the distinction be recognised between the actions of self and other. Using an ingenious approach in which two macaque monkeys monitored each other's actions, Yoshida et al. (2011) identified neurons in medial frontal cortex that selectively encode actions that are taken by the other.

< insert figure 6 about here >

The neural processing models portrayed in figure 6 appear highly consistent with the more detailed review of ape and social learning capacities we reviewed earlier. The consistency is perhaps most obvious in the case of the social learning portfolio we described for chimpanzees. The only real difference is that while Hecht et al. adopt the common view in neuroscientific works (e.g. Tramacere et al. 2016), we have summarized the evidence that imitation is shown by at least some monkeys. However, we suggest that in fact there is no real disagreement here, because (i) the monkey cases all involve transitive actions, as noted above; and (ii) the dorsal stream is not absent in the monkey brains; rather, the proportion of dorsal to ventral white matter is simply less. This fits entirely with our portrayal of the current picture of social learning in monkeys, apes and humans.

4.3 Imitation, autism and the human mirror neuron system

An autistic spectrum disorder (ASD) is a condition marked by often quite severe disturbances in relating socially to others. Through the last several decades, ASD has been attributed to deficits and delays in social cognition, notably mindreading or theory of mind, which has become a dominant explanatory factor (Frith and Hill, 2003). However others noted early difficulties in imitation too, and developed a theory that such deviations from normal development may represent the first stages in difficulties in translating between the perspectives of others and oneself, a fundamental process that underlies both imitation in its earliest stages, and theory of mind as it becomes elaborated through the childhood years (Rogers and Pennington, 1991).

As noted earlier, studies from Iacoboni et al. (2001) onwards have identified imitation as one of the functions served by the mirror neuron system in humans. Noting this and the evidence of early problems in imitation in autism, Williams et al. (2001) put these findings together and suggested that at the core of ASD might be some non-normal developments in the mirror system, possibly including the inhibitory controls implicit in it. The latter is emphasized because on the one hand, the downstream effects of premotor mirror neurons firing need to be inhibited, or we should all be constantly mimicking the actions of those we are watching; and on the other hand, although children on the autism spectrum may show deficits in imitation, they also often display behavior like echolalia, where they simply echo back things that are said to them in an uninhibited fashion.

This theory was suggested as a prospect to explore. It has been contentious, with disputes about both the reality of imitation deficits and delays in autism (Williams et al. 2004; Vanvuchelen et al. 2013) and the explanatory role of the mirror neuron system (Williams et al. 2007; Southgate and Hamilton, 2008). However a recent review by Perkins et al. (2010) concluded that “evidence from functional MRI, transcranial magnetic stimulation, and an electro-encephalic component call the *mu* rhythm suggests MNs are dysfunctional in subjects with ASD” (p. 1239). Problems may entail not so much the basic function of mirroring as the control of such processes, as alluded to above. For example, Martineau et al. (2010) concluded that “hyperactivation of the pars opercularis (belonging to the MNS) during observation of human motion in autistic subjects provides strong support for the hypothesis of atypical activity of the MNS that may be at the core of the social deficits in autism” (p. 168).

5. Concluding Discussion

We have offered a review of progress in the study of primate social learning at several levels the phenomena span, from the underlying mechanisms to the scope of traditions and cultures in wild populations. As we hope to have demonstrated, the research literature has burgeoned in all these domains in recent years and we now know a great deal about each of them, even though in many cases we have extensive knowledge for a handful of favoured species but know little concerning a majority of

primates. Nevertheless, we have accumulated much secure knowledge based on solid and rigorously researched studies, whether from purely observational approaches, or tightly designed experiments. Neuroscientific analysis of social learning and cultural transmission are much younger sciences and still in their early stages. On the one hand, the ‘macro’ analyses of the correlates of encephalization appears to remain highly contentious and difficult to interpret; while at the more detailed level of neural networks and mirror neurons, the empirical literature remains small, particularly for apes (Hecht et al. 2013a,b; Tramacere et al. 2016).

Mindful of the latter, we have focused our review of social learning on relatively complex levels of social cognition that cover imitation and emulation, in part because of the theme of the current issue of the journal and in part because of the neuroscientific relevance of ‘mirroring’ others. In relation to our highlighting here of the topic of bodily imitation, we note that our review suggests that the methodological and evidence base for apes is often different to that for monkeys.

Thus, for apes we have a cluster of ‘Do-as-I-do’ studies that are important in exploring the range of bodily matches that apes can register. This approach, not so far achieved for monkeys, allowed an extensive range of action matchings to be systematically tested, demonstrating, for example that touches to non-visible body parts like the back of the head can be copied, and that apes often begin their copying attempt by repeating one of the approximating training actions, then adjusting it to generate a better match (Custance et al. 1995). Similarly, the motor mimicry subjected to micro-analysis in the case of chimpanzees learning to nut-crack has no counterpart we are aware of in monkeys. Nor have the ‘ghost’ conditions applied in several ape studies been applied in monkey experiments, although the condition in Subiaul et al. (2004) in which a sequential pattern of images was displayed without a monkey touching them may be regarded as formally similar even if physically quite different approach. Finally, ape experiments in which the sequential or hierarchical structure of complex actions has been manipulated (Whiten et al. 2003) appear to have no counterpart in monkey studies, although this takes us beyond bodily matching.

However, monkey studies also include approaches yet to be replicated for apes. Arguably the key method is two-action studies where the two alternatives involve differences at a bodily level, such as completing an action using one’s hands versus a

different effector, like mouth or head. As noted earlier, this approach has been used more generally in comparative psychology but, perhaps strangely, not with apes. Of course the Do-as-I-do method involves all kinds of body-part matching, but it is a test of what apes *can* do, rather than what they spontaneously *do*, which is what has been tested in monkeys and other animals. The precise bodily trajectory matching identified by Voelkl and Huber (2007) also has no apparent counterpart in ape studies and indeed may be a unique application of this approach. The same may be said of the method used by Subiaul et al. (2004) to identify what they called ‘cognitive imitation’ in macaques, but this was expressly not concerned with bodily imitation.

One of the few methods that have been applied to both monkeys and apes is assessing their recognition of being copied by others, and such recognition has been demonstrated for both. However in this case, apes and monkeys still appear to respond differently. Apes have demonstrated this recognition in what we may regard as an explicit fashion, appearing to be intrigued by the bodily matching of their imitator, and experimenting with their own actions to see what copies the other (human) individual delivers. Monkeys have not shown such responses, and their recognition of being copied has been assessed more indirectly, by their visual attention and subsequent affiliative behaviour. Perhaps apes’ explicit responses reflect the same underlying representation of the act of imitation that underlies their capacity to learn the Do-as-I-do game.

Despite the differences in how imitation has been investigated in apes and monkeys, in each case multiple methods have been applied, providing some degree of convergent evidence on the reality of the imitative capacity of interest, and as discussed in section 4.2.3, there is some recent exciting convergence with non-invasive neuroscientific studies with apes, as well as monkeys. Some of the experimental methods, such as Do-as-I-do, have been applied to both apes and monkey but found not to be workable. Others, such as two-bodily-action experiments, should in principle be applicable to both. We hope that some of the varied and ingenious behavioural and neuroscientific approaches we have reviewed, not only with respect to imitation but to the many other aspects of social learning traditions and culture, will be applied more broadly in future and help build a more comprehensive comparative analysis of primate social learning. We close by noting that the subtitle of ‘The Primate Mind’, edited by de

Waal and Ferrari (2012) – ‘Built to Connect with Other Minds’ - is apt to our topic, but also reminds us that this umbrella term covers several related topics beyond the scope of our review, such as empathy and the recognition of states of mind in others. Such topics are also, of course, the focus of other contributions to this special issue.

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Figure Captions

Fig. 1. Group size and encephalization (here, executive brain ratio = volume of cortex over rest of brain) in primates (based on Dunbar and Shultz, 2007).

Fig. 2. Social learning and encephalization in primates. Frequency of social learning based on the survey of Reader and Laland (2002) is plotted against executive brain ratio (see text for further explanation). Added labels refer to three species with complex cultures discussed in the text.

Fig. 3. An ‘open diffusion’ study with capuchin monkeys: (a) capuchin performing ‘lift’ technique on artificial doorian fruit; (b) capuchin performing alternative ‘slide’ technique to gain reward; (c) spread of each technique in groups where one male was first taught to use either the lift or slide technique (data from Dindo et al. 2009). Each symbol represents the proportion of each technique performed by each individual on consecutive days. Dark = slide, light = lift. Numbers indicate the percentage of actions performed on day 7, corresponding to that seeded in the group on day 1.

Fig. 4. Entrainment of nut-cracking between observer and model. Example of frame-by-frame measures of the height of the hand shown for model (blue) and younger observer (red). Time series analyses of such episodes confirmed matching and even synchronic entrainment of hitting actions (based on Fuhrmann et al., 2014).

Fig. 5. Bodily imitation of manual versus oral opening of ‘aethipop’ artificial fruit by vervet monkeys. Most monkeys, and most models, opened aethipops orally (a). In Hammer group, the model opened it with her hands (b) and graphs show corresponding behavior of other group members (d: first attempts with hands, e: all attempts with hands, based on van de Waal et al., 2012). In a further group, an individual opened aethipops using a third method (c) that also spread: see van de Waal et al. (2012) for details.

Fig. 6. Model linking species differences in mirror system circuitry, mirror system functional responses, and social learning, after Hecht et al. (2013a) with permission. PFC: Prefrontal cortex; MLF-ILF: Middle and inferior longitudinal fasciculi; SLFIII: Third branch of the superior longitudinal fasciculus; EmC-ExC: Extreme capsule and external capsule. For further explanation and discussion, see text.

Table 1. Core studies reporting evidence for primate cultural variation in behaviour in the wild.

Species and Year	Studies and outline of evidence	References
Chimpanzee 1999	Building on earlier cited foundational studies, consortium of research leaders at 9 long term study sites completed first collaborative and systematic study, identifying 39 behaviours as cultural variants, common at some sites yet absent at others without apparent environmental or genetic explanation, (1,2). Further detailed studies of specific behaviours and ecological variables, including neighbouring communities, added finer supportive evidence (e.g. 3-7). Experiments highlighted local differences in cultural cognition (8-9).	1. Whiten et al. 1999 2. Whiten et al. 2001 3. McGrew et al. 2001 4. Crockford et al. 2004 5. Möbius et al. 2008 6. Schöning et al. 2008 7. Luncz & Boesch 2014 8. Gruber et al. 2011 9. Kuhl et al. 2016
White faced capuchin 2002	Comparison of different groups recorded the emergence, spread and loss of social customs involving intimate finger poking in nose and eyes (1), plus differences in foraging habits (2) and interspecies interactions (3).	1. Perry et al. 2003 2. Panger et al. 2002 3. Rose et al. 2002
Orangutan 2003	Replication of the chimpanzee methodology (1,2 above) identified 19-24 cultural variants (1) with more reported later (2). More detailed analyses of genetic and habitat variables identified some variants to be linked to environmental differences but strengthened conclusions about a cultural subset (3).	1. van Schaik et al. 2003 2. van Schaik 2009 3. Kruzen et al. 2011
Bonobo 2003	Application of the chimpanzee methodology identified a small set of cultural variants including few forms of tool use, unlike chimpanzees, but range of bonobos much smaller.	Hohmann & Fruth 2003
Olive baboon 2004	Death of dominant males through disease led to peaceful forms of social interaction that continued to reign as new males populated the group, leading to inference of local 'pacific culture'.	Sapolsky & Share 2004
Japanese macaque 2007	34 styles of 'stone handling', an apparently functionless behaviour among provisioned monkeys, were identified, with different ones common or absent at different locations (1). Origin and spread of stone handling was earlier documented (2). Early reports of 'protocultural' behaviours like wheat sluicing are debated (3).	1. Leca et al. 2007 2. Huffman 1996 3. Hirata et al. 2001
Spider monkey 2011	Following chimpanzee methodology (1,2 above) 22 variants identified between different groups, a majority social (1). Further study identified 14 additional behaviours differentially locally preferred, 6 of them inferred to be socially learned (2).	1. Santorelli et al. 2011a 2. Santorelli et al. 2011b
Vervet monkey 2014	Differences in dietary preferences were identified between neighbouring groups that were not explicable by habitat and availability variables measured.	Tournier et al. 2014
Gorilla 2016	Following chimpanzee methodology (1,2 above) 23 putative cultural variants identified between different groups.	Robbins et al. 2016

Studies are listed chronologically by year of foundational paper; for well-studied species, other references listed are selective rather than comprehensive.

1648 Table 2. Cultural diffusion experiments with non-human primates since the first field
 1649 experiments (2010).

authors	species	design	content and findings
van de Waal 2010	vervet monkey *	group seeded	Trained opening of an artificial fruit by models either lifting one door or sliding another spread to others in the groups so long as the model was a resident female.
Kendal et al. 2010	ring-tailed lemur *	group seeded	An idiosyncratic technique to obtain food from an artificial fruit emerged in a subset of lemurs that were close associates, implicating social learning.
Horner et al. 2010	chimpanzee	group seeded	Trained posting of tokens in two different receptacles to obtain food by reliable high ranking models spread to others in preference to those posted by low ranking models.
Hopper et al. 2011	chimpanzee	group seeded	Trained trading of either of two types of tokens to obtain food spread to others even when the option shown gained less quality rewards.
Dindo et al. 2011	orangutan	chain	Each of two different methods to open an artificial fruit (lift door versus slide door) spread preferentially along chains of five and six individuals respectively.
Schnoell et al. 2012	red-fronted lemur *	group seeded	Individuals preferred whichever of two alternative techniques to open an artificial fruit was shown by a trained model in their group and in one of two unseeded groups a stable tradition focused on one technique emerged.
van de Waal et al. 2012	vervet monkey	group seeded	Four groups with model trained to open artificial fruit in each. Most used mouth to open fruit, but in group with model showing manual opening, this method spread to be more common; in group using cord to pull fruit apart, this likewise spread.
Dean et al. 2012	chimpanzee, capuchin monkey	group seeded	An artificial fruit with three escalating levels of difficulty and reward was made available. In conditions where models proficient in the highest level were introduced, these did not spread, unlike in children in parallel experiments.
Hopper et al. 2013	squirrel monkey	group seeded	Groups seeded with trained models pushing a door left or right to obtain food tended to adopt the method witnessed. Monkeys exposed instead to a 'ghost control' in which the door moved without an agent did not succeed in gaining rewards.
Claidiere et al. 2013	squirrel monkey	group seeded	Two groups with model trained to open artificial fruit by lift versus swing door. These methods spread differentially with a bias for those well connected in the social network to open the fruit earlier and use the method they witnessed.
van de Waal et al. 2013a	vervet monkey	group seeded	Four groups with model trained to open artificial fruit in each. Methods of lifting door versus sliding left or right spread more commonly in the group corresponding to seeded model.
van de Waal et al. 2013b	vervet monkey *	group seeded	Whole groups were trained to avoid either pink or blue coloured maize corn made bitter. Naïve infants later tested with no bitter additive nevertheless copied maternal preference. Immigrant males switched quickly, conforming to new group preference.
van Leeuwen et al.	chimpanzee	group	Chimpanzees that had individually learned to use

2013		seeded	either of two alternative tokens to gain rewards, or in other experiments use either of two targets for tokens, did not change their token use when exposed to a majority using the other option (they did not conform to a majority) but did switch when the alternative yielded a great payoff.
Schnoell et al. 2014	red-fronted lemur *	group seeded	Some individuals in groups seeded with either of two methods to obtain food from an artificial fruit maintained the seeded preference over two years, others fluctuated in showing a preference or none, but none switched between preferences.
Gunhold et al. 2014a	marmoset *	group seeded	Naïve individuals tended to adopt whichever of two alternative techniques to open an artificial fruit that the remainder of the whole group had learned X months earlier and maintained the preferences Y months later.
Gunhold et al. 2014b	marmoset *	group seeded	Groups seeded with alternative foraging techniques through video displays in the forest exhibited associated bias in spread of these.
Claidiere et al. 2014	Guinea baboon	chain	Patterns of pixels on a screen remembered by subjects became the stimuli for next animal in chain. Patterns became progressively structured, described as cumulative cultural transmission. Different lineages developed different regular patterns.
Kendal et al. 2015	chimpanzee	group seeded	Statistical models fitted to the results of open diffusion experiments with two alternative techniques to obtain food seeded from trained models
van de Waal et al. 2015	vervet monkey *	group seeded	Replication of 2013 van de Waal et al. paper with wild vervet monkeys. Lift door and slide door methods spread preferentially in groups seeded with these methods.

Primate diffusion studies 2010-2015 (n = 19) from within a set of 30 for all animal species listed in Whiten et al. 2016. * = field study of wild subjects (n = 8); 'group seeded' = open diffusion with trained model(s) seeded in group(s); 'chain' = diffusion chain. Effects are reported when statistically significant.

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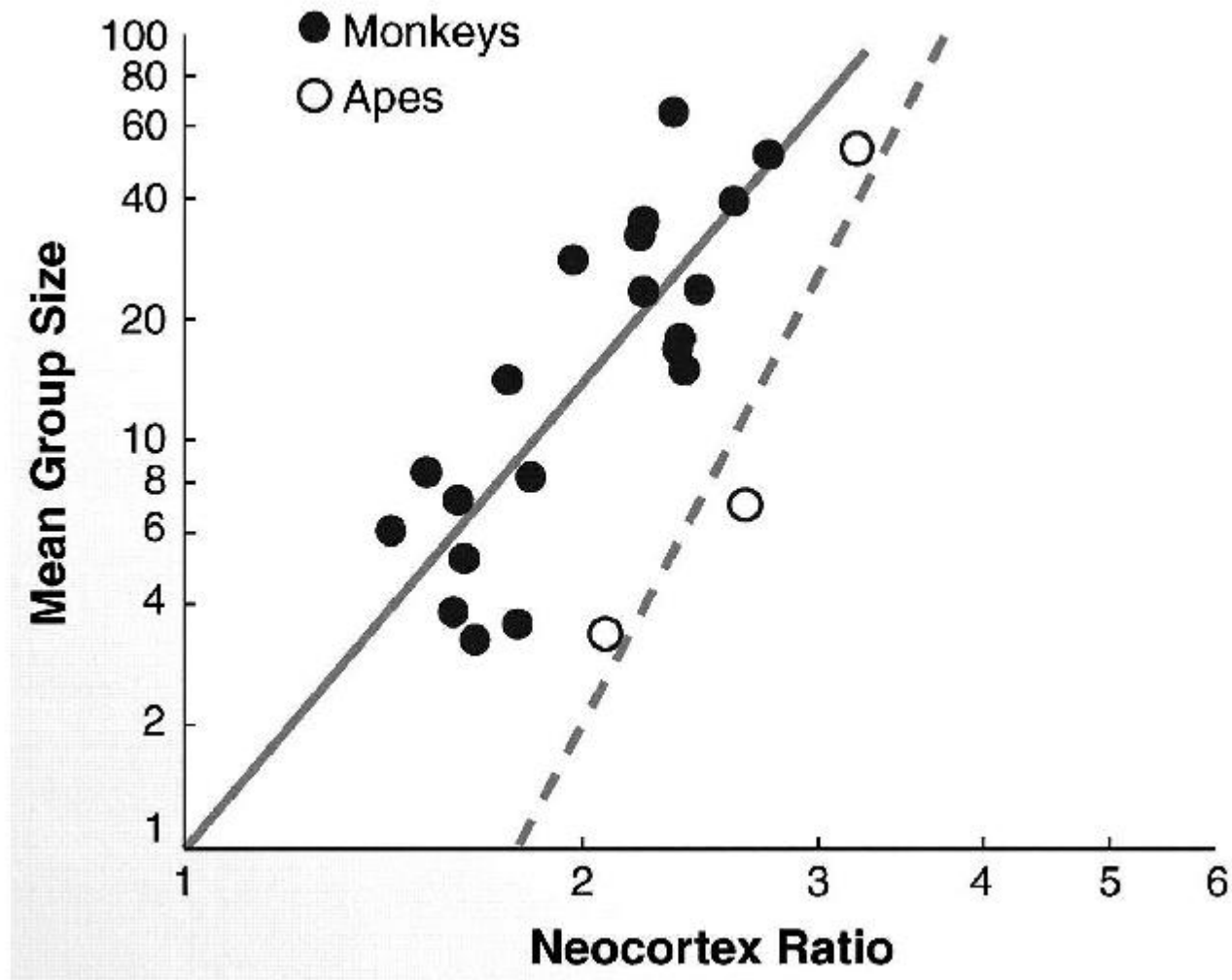


Figure 1

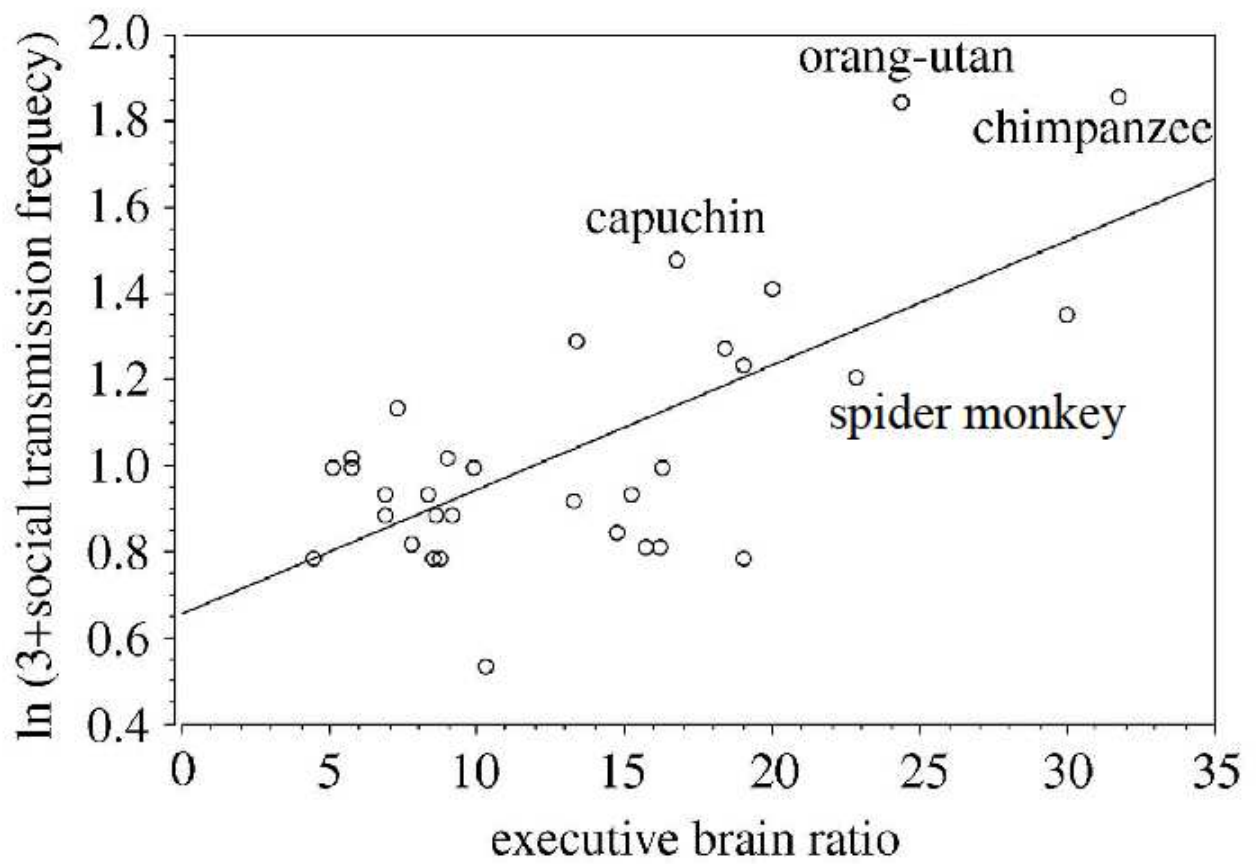


figure 2

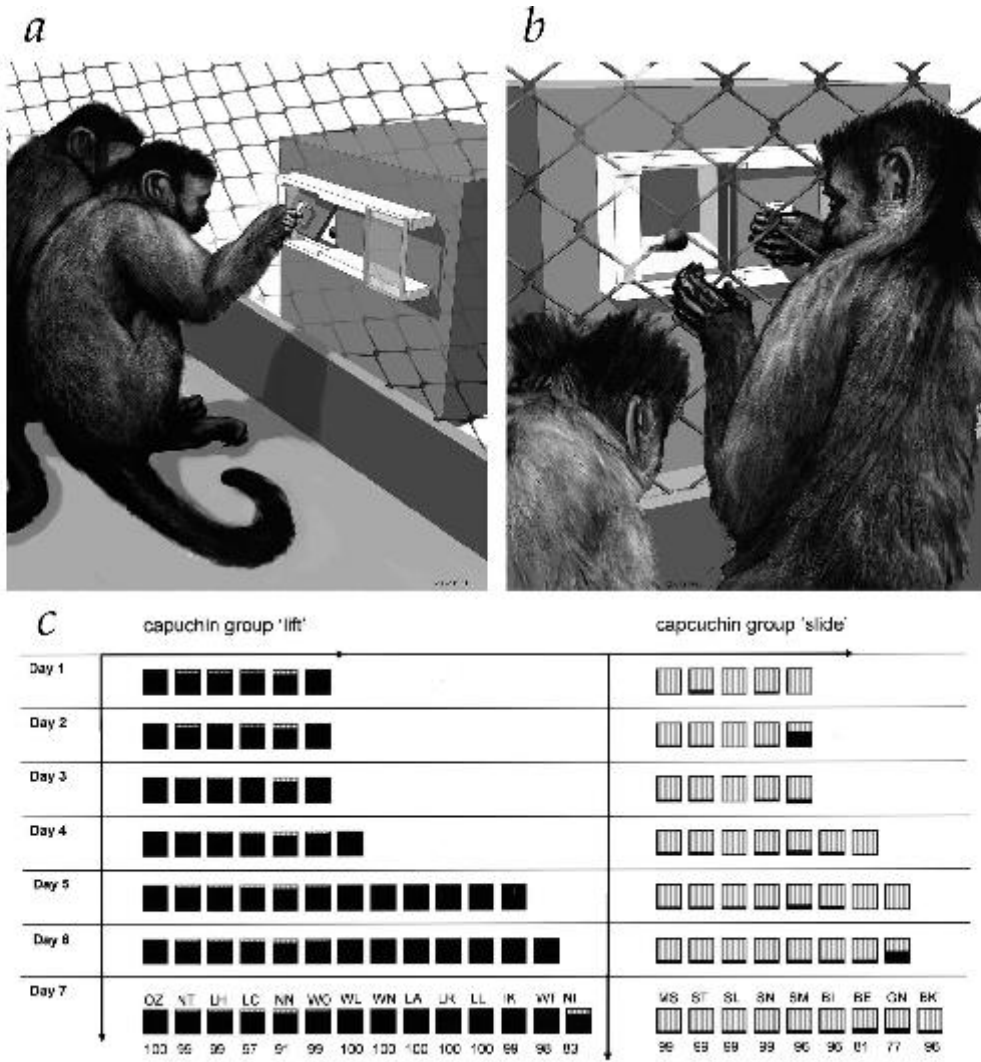
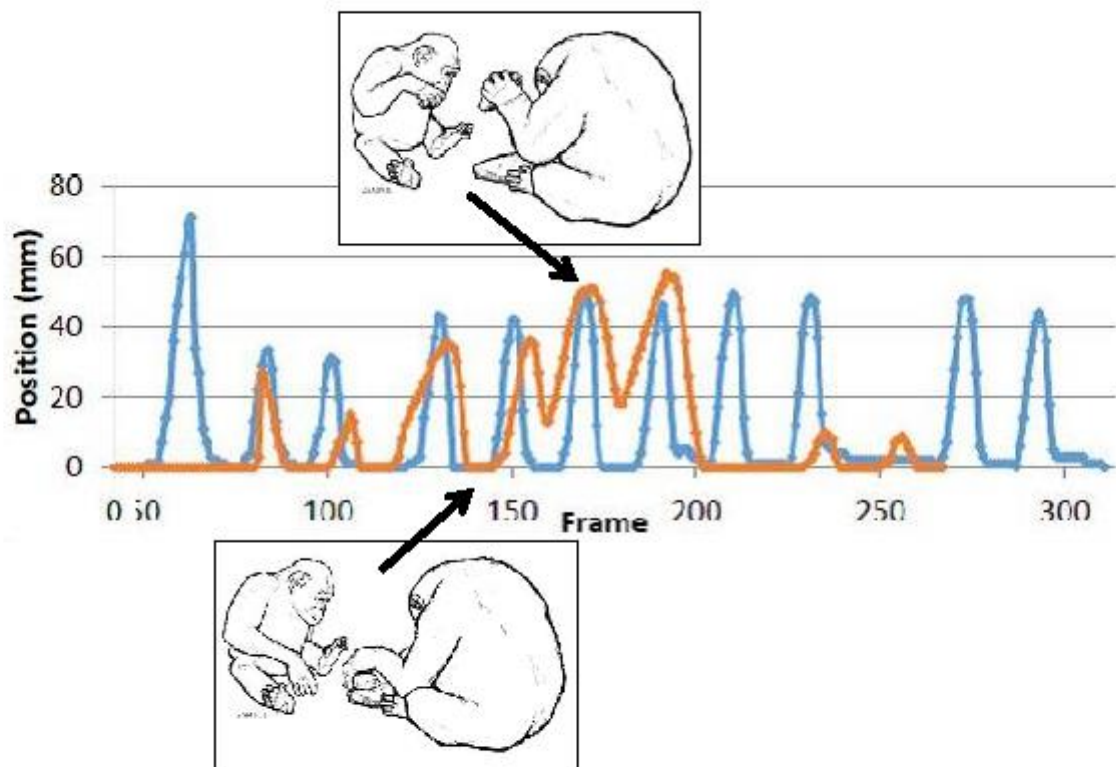
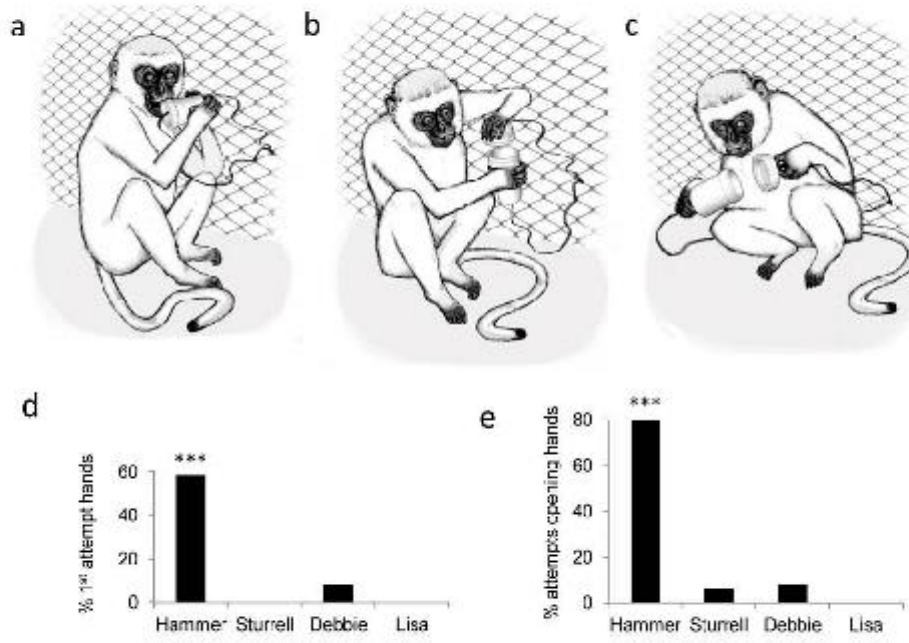


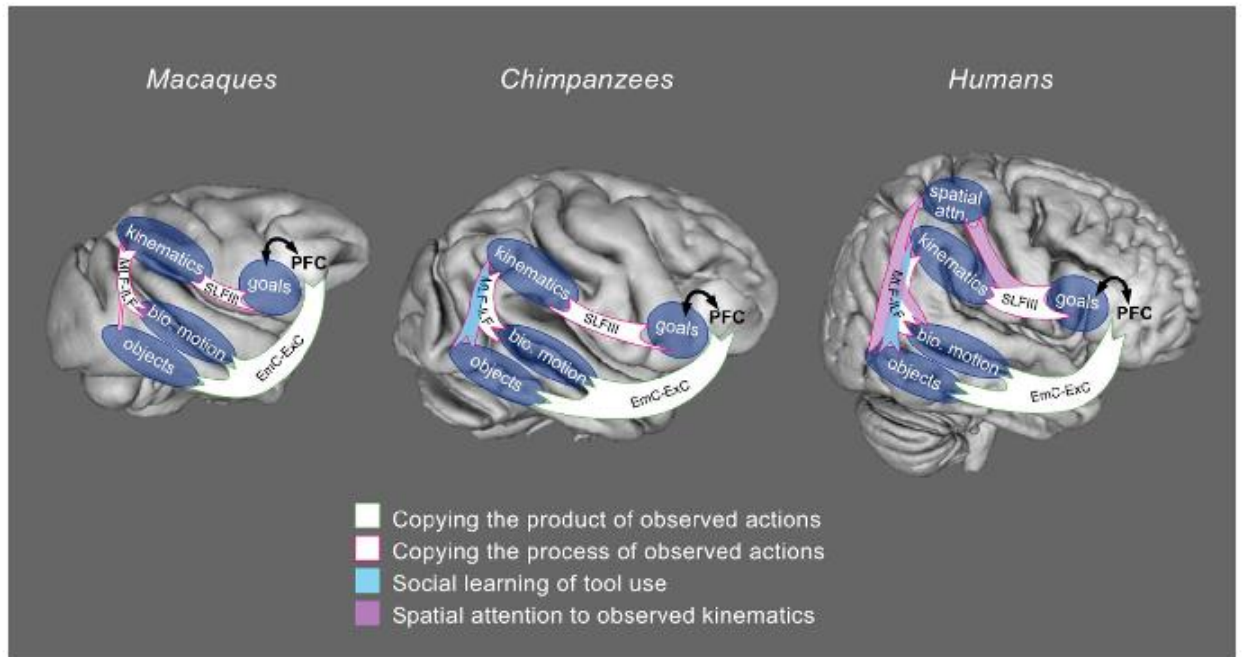
figure 3



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